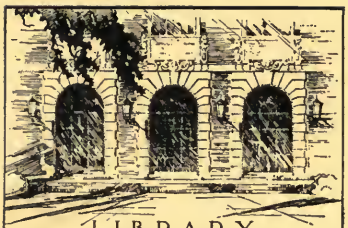

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TRACHYTHERUS, A TYPOTHERID FROM THE DESEADO BEDS OF PATAGONIA

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RESULTS OF THE FIRST MARSHALL FIELD PALEONTOLOGICAL EXPEDITION TO ARGENTINA AND BOLIVIA, 1922-24

Trachytherus[1] is one of the most important of the earlier genera of typotheres but, due to lack of adequate specimens, its affinities have been in doubt for over forty years. Generally it has been either referred to a distinct family, under the invalid name Eutrachytheridae, or placed, with reservations, in the Typotheriidae. The First Marshall Field Expedition collected a partial skull of *T. spegazzinianus*. This specimen, when studied together with others collected by the Amherst College Expedition and the Scarritt Patagonian Expedition, provides a much better conception of relationships than has been possible hitherto. The view here defended is that *Trachytherus* is a member of the Typotheriidae and possibly, although not certainly, ancestral to the later members of the family. The present communication is confined to a short account of such morphological characters as are of value in determining affinities; detailed description is deferred until the publication of the final memoir on the Typotheria of the Deseado and Colhué-Huapí beds. It will be noted that in the text *Trachytherus* is more often compared with *Pseudotypotherium* of the Monte Hermoso than with *Typotherium*. The reason for so doing is that an original specimen of the Monte Hermoso genus is available for comparison. The differences between the two genera are, however, so slight that almost all statements made for one are equally applicable to the other.

I wish to express my thanks to Professor F. B. Loomis and to the authorities of the American Museum for the privilege of studying specimens from their collections. The preparation of the Field Museum material has been skillfully performed by Mr. J. B. Abbott.

[1] Usually known as *Eutrachytherus*. Ameghino proposed this name in 1897 in the belief that *Trachytherus* was preoccupied by *Trachytherium* Gervais, 1849.

The drawings are by Mr. Carl F. Gronemann, Staff Illustrator of Field Museum.

Trachytherus spegazzinianus Ameghino.

Trachytherus spegazzinianus Ameghino, F., 1889. *Trachytherus spegazzinianus*, nuevo mamífero fósil del orden de los toxodontes, Buenos Aires, pp. 1–8.

I recognize but one species of the genus. The two extremes in size which have been regarded as distinct species; namely, *T. conturbatus* Ameghino (1891, p. 241) and *T. grandis* (Loomis) (1914, p. 82), are fairly evenly connected by the specimens at hand and by the specimens described and figured by Ameghino (1889B, pp. 918–919, Plate 79, Figs. 1, 2). Nearly all the material in North American institutions comes from the same level at one small locality, Cabeza Blanca in the Province of Chubut, a fact which increases the probability that there is only one valid species despite the rather wide range in size. A further discussion of this question and a table of measurements will be given in the memoir.

MORPHOLOGY

DENTITION

The dental formula is $\frac{3}{2}, \frac{0-1}{1}, \frac{4}{4}, \frac{3}{3}$; the first and second upper incisors, the canines, and the first premolars are small, separated by diastemata, and of little functional importance.

Upper teeth.—The first incisor is greatly enlarged (although not as large, relatively, as in *Typotherium*), arched and hypsodont; the grinding surface is irregularly triangular in outline. The antero-posterior diameter of the tooth is greatest at the mesial side, the labial and lingual faces converge laterally. The enamel is confined to the gently convex labial surface. The small second and third incisors, the canine, and P^1 are of interest only on account of their vestigial condition.

The structure of unworn premolars has been described previously by me (1934B, p. 101); the rather complex crown pattern is shallow and disappears rapidly as abrasion proceeds. The teeth of this series are at first pentagonally shield-shaped in outline, but later each assumes the contour of a parallelogram (figs. 24*a*, 25). The grooves on the lingual sides, which are persistent in *Pseudotypotherium* and *Typotherium* disappear rather early in *Trachytherus*.

A particularly valuable feature of the series of specimens at hand is that nearly all stages in the wear of the molars are represented. These age variations are of considerable value in judging the affinities

of the genus but, due to lack of sufficient material, their significance has not been fully appreciated hitherto. Each molar on erupting is narrow transversely and composed of three approximately subequal lobes extending internally from the ectoloph. The homologies of these lobes have been discussed previously (Patterson, 1934B,

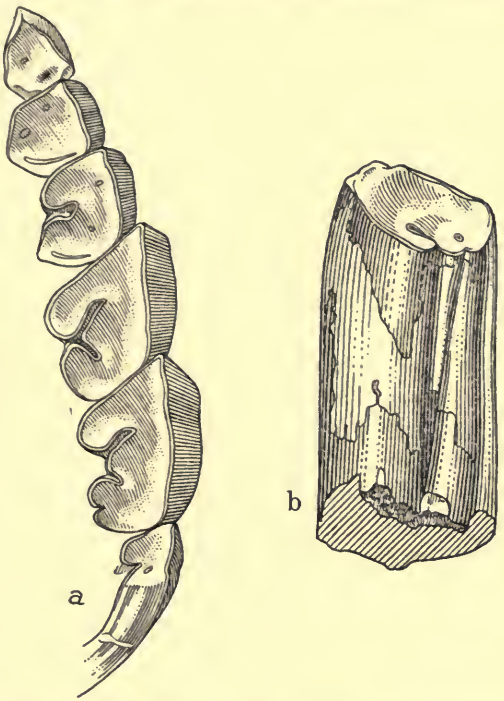

FIG. 24. *a*, *Trachytherus spegazzinianus* Ameghino. P^2–M^3, A.C.M. No. 3264. x 1/1. *b*, *Trachytherus spegazzinianus* Ameghino. M^3, showing gradual decrease in size of median lobe, F.M. No. P13381. x 1/1.

p. 102, fig. 18). At this stage the molars are very similar to those of *Pseudotypotherium*. As abrasion proceeds the transverse diameter increases and the median lobe steadily decreases in size (fig. 24*a*) until there is a close resemblance to molars of interatherids such as *Cochilius* and *Plagiarthrus* (=*Argyrohyrax*). This fact supports the previously advanced thesis that the median lobe is formed from a united crista and crochet. In still older individuals (fig. 25) all traces of crown structure are lost on M^1 which finally assumes the parallelogram-like outline of deeply worn premolars. It is possible, but not yet demonstrated, that the same would be true for M^2–^{3}. An isolated third molar (fig. 24*b*) is very instructive in that it clearly shows the gradual decrease in size of the median lobe

and its envelopment by the anterior and posterior lobes. Despite the great age variation displayed there is no evidence that the teeth, excepting the vestigial ones, developed roots during life.

Lower teeth.—There are no specimens of the mandible in North American collections. The following statements are based on photographs of a specimen in the Ameghino Collection kindly furnished by Professor Scott, and on Ameghino's description (1897, p. 429). The two pairs of incisors, of which the internal is somewhat the larger, are proclivous and slightly grooved on the lingual side, as in *Typotheriopsis*. It is very much smaller than the corresponding tooth in *Typotherium*. The canine (this tooth could be $I_{\overline{3}}$) and $P_{\overline{1}}$ are vestigial and rooted. The last three premolars are molariform; $P_{\overline{2}-\overline{3}}$ are probably hypsodont but this point cannot be determined with certainty from the photograph. The molars steadily increase in size posteriorly and are essentially similar in structure to those of the Pleistocene genus.

Derivation of the dentition of the later typotherids from the *Trachytherus* type would necessitate the following changes in the intermediate forms: (1) further enlargement of $I_{\overline{1}}$ and diminution of $I_{\overline{2}}$; (2) elimination of I^2–P^2 and C–$P_{\overline{3}}$; (3) persistence of the lingual groove of P^3, P^4, and increase in size of the median lobe of the upper molars. Acquisition of these characters by the intermediate forms would require no radical departure from the structure seen in *Trachytherus*. I^2–P^1 and C–$P_{\overline{1}}$ are already greatly reduced. As will be pointed out below (p. 125), the necessary increase in size of $I_{\overline{1}}^1$, elimination of $P_{\overline{2}}^2$–$_{\overline{3}}$, and enlargement of the median lobe of the molars could have taken place in correlation with progressive enlargement of the masseter muscles, modification of the anterior portions of the zygomatic arches, and consequent convergence toward a rodent-like habitus. *Trachytherus*, in fact, presents an ideal starting point for the specialized arch structure of *Typotherium*.

SKULL

The skull of *Trachytherus*, although essentially similar to that of *Pseudotypotherium*, is more primitive in several respects. The facial region is considerably longer than that of the later genus, the rostrum is tapering, the post-orbital processes are slightly smaller, and the nasals do not extend as far posteriorly. The occiput is not as wide and the occipital crest is rather deeply notched in the median line, whereas it is straight in *Pseudotypotherium; Typotheriopsis*, however, resembles *Trachytherus* in this character. The posterior faces of the palatines and pterygoids are narrower transversely and

there is much less flexure of the basifacial axis upon the basicranial. The zygomatic arches of *Trachytherus* and *Pseudotypotherium* are very different but, as explained below, I believe that the arch of the later genus was derived from the type of the earlier, and that gradual acquisition of the *Pseudotypotherium* type of arch by the inter-

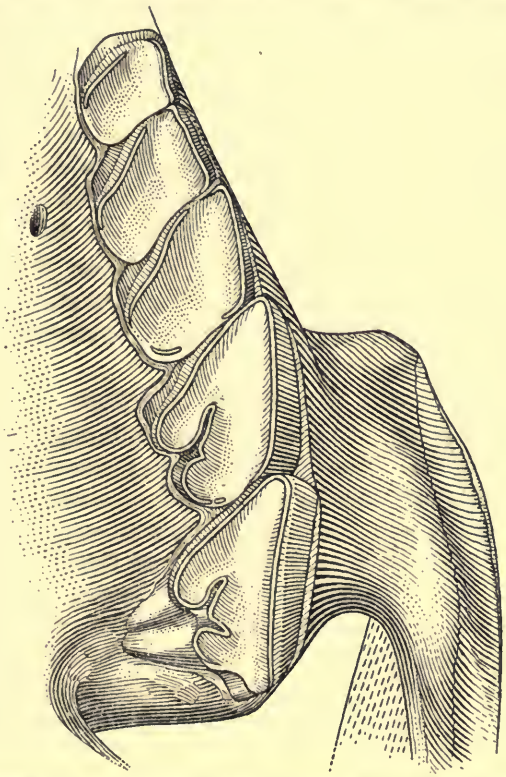

FIG. 25. *Trachytherus spegazzinianus* Ameghino. Cheek-teeth and zygomasseteric structure, F.M. No. P13281. x 1/1.

mediate forms would also involve some of the differences listed above. The auditory regions of the two are similar (p. 126).

Zygomatic arch.—In *Trachytherus* the anterior root of the arch is stout; it is situated opposite M^{2-3} on the old individual shown in fig. 25, but on the younger specimen figured and described by Loomis it is opposite M^{1-2}. The jugal is of the normal toxodont type, i.e., it extends dorsally upon the face in a strip which meets the triangular lachrymal and excludes the maxillary from the anterior rim of the orbit. The maxillary takes a large part in the zygomatic structure. It forms the inner portion of the anterior half of the arch, coming in

contact with the squamosal posteriorly. Anteriorly this bone forms a small, rounded protuberance beneath the anterior rim of the orbit. This structure is regarded as the homologue of the better developed descending process of the interatherids (p. 135). The area of origin of the masseter muscle is on two planes. The area for the pars lateralis (employing the terminology used by Miller and Gidley for the rodents[1]) is situated beneath the orbit and extends forward and slightly upward as far as the short descending process of the maxillary. The area for the pars medialis apparently extends from the anterior root of the zygoma upward and backward to the zygomatic process of the squamosal. The area for the pars lateralis is slightly flaring, the flare being considerably more prominent on the old specimen shown in the figure than on the younger one figured by Loomis.

On the one hand *Trachytherus* foreshadows *Pseudotypotherium* in the slightly flaring area of origin for the masseter lateralis, and on the other resembles the interatherids in the possession of the slight descending process of the maxillary.

In *Pseudotypotherium* (fig. 26) the maxillary no longer touches the zygomatic process of the squamosal, although it still takes an extensive part in the formation of the inner side of the anterior half of the arch. Anteriorly there is no descending process of the maxillary. This bone, together with the jugal, forms a broad, concave zygomatic plate which extends obliquely upward and forward in front of the orbit for the accommodation of the enlarged masseter lateralis. The medialis origin is poorly defined and this part of the muscle was probably rather weak. The lateralis origin in this genus thus shows a strikingly close resemblance to the zygomasseteric region of many sciuromorph rodents and is markedly different in appearance from that in *Trachytherus*.

As stated, however, it seems likely that the zygomasseteric region of *Pseudotypotherium* is structurally derivable from the *Trachytherus* type. The difference between the two genera seems to be one of degree rather than of kind, the slight flare of the masseter lateralis origin of the earlier genus being the rudiment of the zygomatic plate which is so prominent a feature of the later form. Conversion of the zygomasseteric region of *Trachytherus* into that of *Pseudotypotherium* would involve only the loss of the small descending process of the maxillary and the progressive enlargement of the flare of the lateralis origin by the intermediate forms. The close resemblance

[1]The pars superficialis lateralis was apparently lacking in members of the family.

between the two genera in the structure and arrangement of the teeth and particularly in the structure of the auditory region (see below) indicates close relationship in my opinion and renders it extremely probable that these changes have taken place.

Evolution toward the zygomasseteric structure of *Pseudotypotherium* by the descendants of *Trachytherus*, or of related forms in

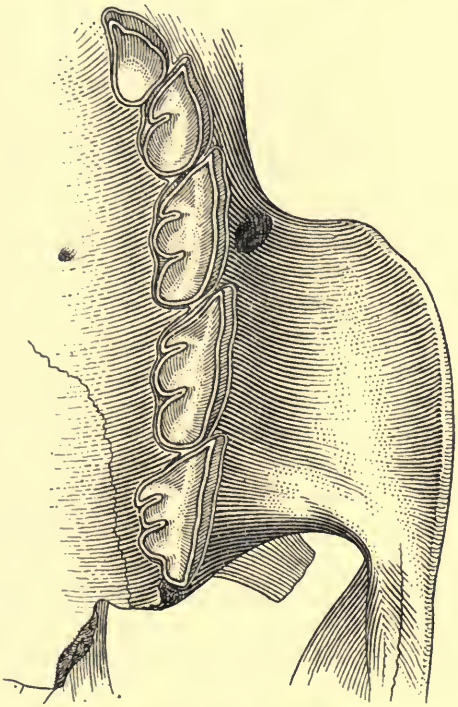

FIG. 26. *Pseudotypotherium pseudopachygnathum* (Ameghino). Cheek-teeth and zygomasseteric structure, A.M. No. 14509. x 1/1.

a comparable stage of development, granting that it took place, involved convergence towards a rodent-like habitus. The results would be that (1) constantly increasing pressure would be put upon the anterior pair of incisors, and (2) constantly increasing stress in mastication would be laid on the posterior cheek-teeth. Thus, *pari passu* with the enlargement of the zygomatic plate, the anterior incisors became progressively enlarged and the rostrum broader, $I_{\overline{2}}$ decreased in size, and $I^{\overline{2}}$–$P^{\overline{2}}$ and C–$P_{\overline{3}}$ were eventually eliminated. The necessity for a maximum area of grinding surface resulted in the progressive enlargement and eventual persistence of the median

lobe of the upper molars. The evolution of the zygomatic plate also involved the development of a shorter, more compact, facial region, and the shifting of the nasals posteriorly.

Auditory region (fig. 27).—Part of the lateral wall, only, of the auditory bulla is preserved. The portion missing corresponds to the entotympanic, the portion remaining to the ectotympanic, of *Typotheriopsis* (Patterson, 1934A, p. 84). The remnant which remains serves to indicate that the depth of the bulla was approximately the same as in *Pseudotypotherium*. The tubular meatus has the same course and relations to the surrounding elements as it has in the Monte Hermoso genus (*op. cit.*). The crista meati is almost identical in the two forms, an important point of resemblance since this element is not developed in either the Hegetotheriidae or the Interatheriidae. The porus is situated on practically the same level as in *Pseudotypotherium;* its ventral border is formed by a lip projecting posteriorly from the crista meati. The vagina processus hyoidei occupies the position usual in the order (Patterson, 1932, p. 23) but differs slightly from that of *Pseudotypotherium* in that a short groove runs antero-internally from it along the lateral wall of the bulla; a similar groove is present on the bulla of *Leontinia*. The epitympanic sinus is identical with that of *Pseudotypotherium*. The foramen lacerum medium and foramen ovale, the foramen lacerum posterius, and the stylomastoid foramen are exactly similar in the two genera. The crista meati of *Trachytherus* is almost as completely fused with the post-glenoid process of the squamosal as is that of *Pseudotypotherium*. The post-glenoid foramen, however, is not situated as far forward as in the Monte Hermoso genus. *Trachytherus* also possesses small vascular foramina situated behind the post-glenoid foramen, a further point of resemblance between the two genera.

ENDOCRANIAL CAST

A very imperfect natural braincast (fig. 28) was obtained by Mr. Abbott while engaged in the reconstruction of the skull shown in fig. 27. Unfortunately no artificial cast was made at the time. Despite its poor preservation the cast is of considerable importance since it shows conclusively that the one referred to this genus by Loomis (1914, pp. 77–80) was incorrectly identified, thus eliminating this very misleading item of evidence. The specimen at hand lacks the olfactory bulbs, most of the dorsal surface of the cerebrum, the vermis and hemispheres of the cerebellum, and most of the medulla.

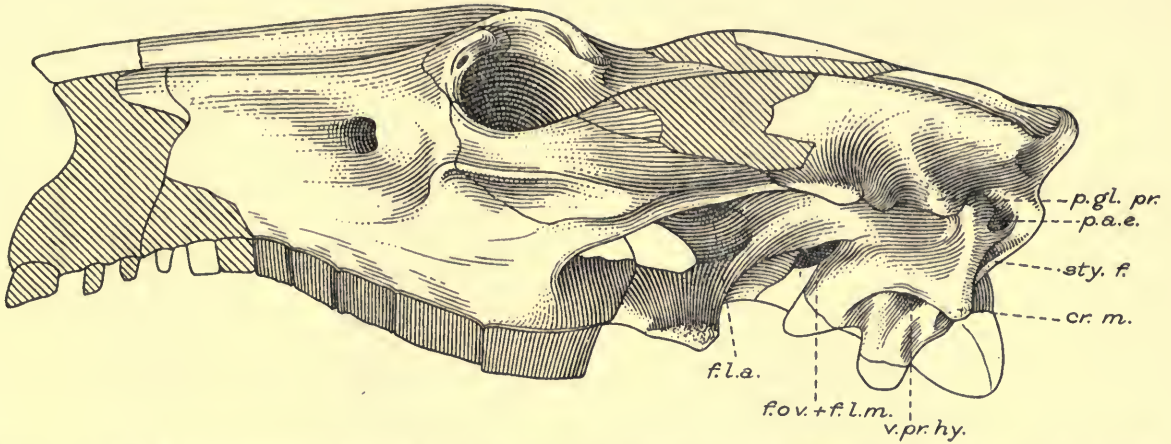

FIG. 27. *Trachytherus spegazzinianus* Ameghino. Skull, lateral view. Note small descending process of maxillary beneath orbit, and incipient zygomatic plate. Cross-hatched areas restored from A.C.M. No. 3264. F.M. No. P13281. x 1/2. *cr.m.*, crista meati; *f.l.a.*, foramen lacerum anterius; *f.o.v.* + *f.l.m.*, foramen ovale and foramen lacerum medium; *p.a.e.*, porus acusticus externus; *p.gl.pr.*, post-glenoid process; *sty.f.*, stylomastoid foramen; *v.pr.hy.*, vagina processus hyoidei.

It has undergone a certain amount of distortion, and some breakage due to fragments of bone having been forced into it during the process of fossilization. In view of this and of the poor general preservation it is possible that the following description may prove

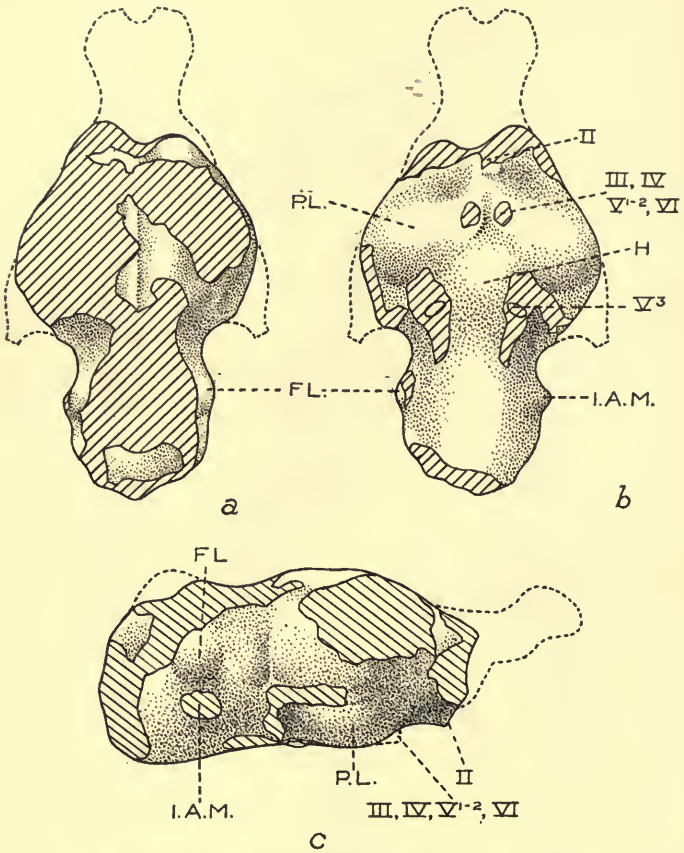

FIG. 28. *a*, *b*, and *c*, *Trachytherus spegazzinianus* Ameghino. Endocranial cast, dorsal, ventral, and lateral views. Cross-hatched areas=broken surfaces. Parts in outline tentatively restored after *Hegetotherium* and *Notostylops*. F.M. No. P13281. x 2/3. II, optic nerves (filling of optic canal); III, IV, V^{1-3}, VI, common canal of these nerves (filling of foramen lacerum anterius); V^3, mandibular nerve (filling of foramen ovale); FL., "flocculus" (cerebellar lobule in petrosal); H, filling of fossa hypophyseos; I.A.M., internal auditory meatus (nerves VII and VIII); P.L., pyriform lobe.

to be incorrect in some details although the principal points are probably correct.

The serial arrangement of the cerebrum and the cerebellum is, so far as can be determined, essentially similar to the conditions described by Simpson (1933B) in *Hegetotherium* and *Protypotherium;*

there is very little flexure. The outline of the cerebrum is roughly triangular; the ratio of cerebrum to cerebellum was probably about 2 : 1. The pyriform lobes are large and expanded mesially to about the same extent as in *Hegetotherium;* they are not visible in the dorsal view. The lobes do not appear to have extended as far posteriorly as the neopallium. The region of the hypophysis is gently convex.

The cerebellum and the cerebrum while not as close to each other as in *Hegetotherium* are considerably closer than in *Notostylops.* The midbrain was possibly exposed to a slight extent. The "flocculus" is circular and prominent. There is no visible marking or convexity in the region of the pons.

Only three of the nerve exits are preserved. The optic nerves appear as though conjoined. The common exits for III, IV, V^{1-2}, and VI are closely approximated, as in *Hegetotherium,* due to the mesial expansion of the pyriform lobes. The internal auditory meatus (VII, VIII) is directly beneath the "flocculus" and is situated well posterior to the cerebrum.

There is no separate opening for the entocarotid as in *Notostylops* and (presumably) *Protypotherium.* The postero-lateral cerebral venous opening, which appears to be typical of the Typotheria and *Notostylops,* is not preserved in the cast but was almost certainly present originally.

The endocranial cast of *Trachytherus,* or at least that part of it which is preserved, appears to be intermediate in development between *Notostylops* (Simpson, 1933A) and *Hegetotherium* and rather closer to the latter. This fact is in keeping with the geologic ages of the three genera. In depth, mesial expansion of the pyriform lobes, size of the neopallium and distance between the dorsal exposures of the cerebrum and cerebellum, *Trachytherus* resembles *Hegetotherium* rather than *Notostylops.* The distance between the "flocculus" and internal auditory meatus and the cerebrum is, however, more nearly comparable to that seen in the Casamayor genus. The braincast of *Typotherium* has so far been figured and described in dorsal view only (Gervais, 1872, pp. 434–436, Plate 21, Fig. 11; Edinger, 1929, pp. 194–195, fig. 184), a fact which does not permit adequate comparison with *Trachytherus.* Nevertheless it can safely be stated that the reference of *Trachytherus* to the Typotheriidae is not opposed by any of its known endocranial characters.

AFFINITIES

Historical review.—In his first publication on the genus Ameghino (1889A) referred it, without comment, to the Typotheriidae. This paper was reprinted without change in his great work on South American fossil mammals (1889B, pp. 918–919). The same author a few years later (1892, p. 276) made the genus the type of the family Trachytheridae but gave no discussion of its relationships to the Typotheriidae.

Lydekker (1894,[1] p. 1) referred *Trachytherus* to the family Typotheriidae, apparently considering it as a connecting link between *Typotherium* and *Nesodon*, and stated that "the genus may probably be regarded as the direct ancestor of *Typotherium;* and as descended from a form more or less closely allied to *Nesodon.*" In his lengthy and very valuable criticism of Lydekker's volume, Ameghino (1895A, pp. 98–100) very properly refuted the theory of relationship between *Trachytherus* and *Nesodon*. He also took exception to Lydekker's statement that the genus is a member of the Typotheriidae and probably ancestral to *Typotherium*. He maintained that the dental formula and the structure of the premolars and molars merited family distinction and indicated that the two families could only be considered as divergent lines from a common ancestry. The Typotheriidae he regarded as possibly descended from the protypotheres (p. 136). In 1897 (p. 427) Ameghino changed the name of the genus to *Eutrachytherus* but gave no further opinion upon its affinities. A few years later (1904, 57, p. 164) in discussing the upper Miocene typotherid *Eutypotherium*[2] (Roth, 1902, p. 256), he stated that this genus approached *Trachytherus* in some characters. In his paper on the astragalar foramen, the same author (1905, pp. 420–423) modified his views of 1895. He stated that it was difficult to determine, due to lack of material from the intervening horizons, whether or not the two families were distinct or whether the Typotheriidae were derived from the "Eutrachytheridae." *Trachytherus* he regarded as much less specialized than *Typotherium* in certain respects but much more so in others. He did not enumerate the characters that might come under the latter category and it is difficult for me to conceive what

[1] The work bears this date on the title page but was apparently not published until early in 1895.

[2] This genus is usually known as *Tachytypotherium*. Roth (1904, p. 158) proposed the latter name upon discovering that Haeckel had employed *Eutypotherium* for a hypothetical genus. According to the rules, however, Haeckel's name has no standing.

they might be.[1] In the characters of the astragalus he recognized that the "Eutrachytheridae" and the Typotheriidae "are so extremely similar that the differences are insignificant."[2]

Loomis in turn described original specimens of the genus. He recognized the family "Eutrachytheridae" and (1914, p. 80) considered that *Trachytherus* probably belonged in the series that terminated in *Typotherium*, but that "such a form as *Argyrohyrax* is more likely to be the really ancestral form." Loomis placed *Argyrohyrax* (= *Plagiarthrus*) in the "Eutrachytheridae" but, as shown previously by me (1932, p. 21) and later in more detail by Simpson (1932A, p. 6), this genus is an interatherid and therefore can hardly be considered ancestral to *Typotherium*.

Simpson (*loc. cit.*) held that the distinctions between the Interatheriidae, Archaeohyracidae, and "Eutrachytheridae" were "by no means so clear cut as one might wish or as Ameghino and Loomis suggested." In a later paper (1933B, p. 18), in which he doubtless had in mind the braincast erroneously identified by Loomis (p. 126), he wrote that the genus was aberrant. Schlosser, in Zittel's textbook, tentatively referred the genus to the Typotheriidae. Scott (1913, pp. 462, 477) placed it in the Typotheriidae.

Relationships with Typotherium.—In the preceding pages it has been shown that the auditory region, general structure of the skull, and the arrangement of the dentition of *Trachytherus* indicate close affinity with *Typotherium*. The humerus and astragalus of the two forms are known to be practically identical in structure. The true braincast of *Trachytherus* has been described and shown to be essentially similar to those of other typotheres and not at all of an aberrant type. The view has been advanced that the differences between the two genera in the facial region, dental formula, and upper molar structure are due to the gradual acquisition by the intermediate forms of a zygomatic plate resembling that of many sciuromorph rodents. *Trachytherus* shows an incipient but important advance toward this condition in that the area of origin of the masseter

[1] It is possible that Ameghino, in accordance with his known views on dental evolution, might have regarded an upper molar with three persistent lobes as more primitive than one in which the median lobe disappeared during the life of the animal. In his paper of 1897 (p. 428) he wrote that the median lobe of the upper molars was "rudimentary." So far as I have been able to gather from his works, Ameghino used the erroneous term "rudimentary," instead of the correct term "vestigial," in referring to structures that he considered to be on the decline.

[2] An incomplete distal half of a humerus was found in association with the skull shown in fig. 27. This specimen agrees in all particulars with those of *Typotherium cristatum* figured by Gervais (1867–69, Plate 22, Figs. 4, 4*a*; Plate 25, Fig. 3), except that it has a stronger ectepicondylar crest.

lateralis is slightly flaring; this character was apparently unknown to Ameghino. Therefore it is maintained that *Trachytherus* may properly be included in the Typotheriidae.

The major difficulty that interferes with a definitive evaluation of the mutual affinities of *Typotherium* and *Trachytherus* was recognized by Ameghino in 1905 and unfortunately still exists today. This is the fact that the history of the family is practically unknown between the Oligocene and the upper Miocene.[1] In view of this a very brief survey of the known genera of the family will be of advantage here. Ameghino (1905, pp. 421–422) referred to the "Eutrachytheridae" two genera from the Casamayor, *Isotypotherium* and *Epitypotherium*, which he described on isolated astragali of the *Trachytherus-Typotherium* type. These scanty remains serve to indicate that the family was already differentiated in Casamayor time, a fact which is not surprising since it is now known that *Notopithecus* (=*Adpithecus*) of this fauna had already acquired the characteristic interatherid type of zygomatic arch (Riggs and Patterson). The Deseado genus *Proedrium*[2] (Ameghino, 1895B, pp. 623–624; 1897, p. 429) differs from *Trachytherus* in having proportionately smaller upper incisors and $I^{\frac{2}{2}}$ triangular and slightly larger than $I^{\frac{1}{1}}$. Ameghino (1906, p. 473) mentioned a form from the Río Teca (a horizon containing an undescribed fauna considered to be transitional between the Deseado and the Colhué-Huapí) which he stated was similar to *Trachytherus*. With the exception of this form, no typotherid is known[3] between the Deseado and the Collon

[1] By upper Miocene is here meant the horizons included by Kraglievich (1930, p. 157; 1934, pp. 119–120) in the Friasian and assigned by him to the middle and lower Miocene. In the writer's opinion Kraglievich assigned too early an age to the various Argentine mammal-bearing formations. Thus he placed (by implication) the Patagonian beds in the lower or middle Oligocene whereas the invertebrates (Ortmann) and particularly the cetaceans (Kellogg) of this formation show conclusively that it is of lower Miocene age. I regard the Uquía formation as lower Pleistocene, the Araucanian-Entrerian series as Pliocene, and the Río Mayo, Río Frías and Collon Curá beds as upper Miocene. The Santa Cruz is probably middle Miocene and the Colhué-Huapí either lower Miocene or upper Oligocene, depending upon whether or not it is really synchronous with part of the marine Patagonian. The Deseado may be regarded as middle or upper Oligocene. The Casamayor is provisionally considered, following Schlosser, to be upper Eocene.

[2] Later changed (Ameghino, 1904, p. 171) to *Isoproedrium* in the mistaken belief that the original name was preoccupied by *Proedrus* Foerster 1888.

[3] The little-known genus *Ameghinotherium* Podestá (1899) from Corruzú-Cuatiá, Province of Corrientes, is of unknown age. I have been unable to see the original description, which was published in a periodical apparently not available in North American libraries. Ameghino (1899, p. 5) has given a very brief summary of characters. The skull and dental formula are similar in general to *Typotherium*, but $I^{\frac{1}{1}}$ and the premaxillary are greatly reduced and a small canine is present. The cheek-teeth are compressed antero-posteriorly and wide transversely, the premolars are simple and elliptical, the molars rectangular and *complicadas*. No mention is made of zygomasseteric structure.

Curá. The specimen from the latter horizon was described as *Eutrachytherus modestus* by Roth (1899, p. 188) on the basis of upper teeth. It is difficult to determine the affinities of this form from the published description; Ameghino (1906, p. 232) has questioned the generic reference. In addition to this doubtful form two genera, *Eutypotherium* Roth and *Typothericulus* (Kraglievich, 1930, p. 148), which have the same dental formula as *Typotherium* are known from the upper Miocene. The former occurs in both the Río Frías and the Río Mayo, the latter only in the Río Mayo.[1] *Typothericulus* is distinguished from *Eutypotherium* by the occurrence of a lingual groove on P^4. This character led Kraglievich to the opinion that the genus was ancestral to *Pseudotypotherium* and *Typotherium*. Nothing is known of the zygomasseteric structure. *Eutypotherium* and its recently described descendant *Typotheriopsis* (Cabrera and Kraglievich, 1931, p. 111; Kraglievich, 1930, p. 146) of the Chasicó and Araucanense appear to be very similar in structure, judging from figures of the former given by Rovereto (1914, Plate 1) and from specimens of the latter in the Field Museum collections. *Typotheriopsis*, although structurally much closer to *Typotherium* than to *Trachytherus*, is nevertheless transitional between the two genera in some characters. The zygomatic plate is well developed but is by no means as large as in the Pleistocene genus. I_1 is smaller and $I_{\bar{2}}$ rather larger than in *Typotherium*. Also, as noted above (p. 123), the occiput is notched medianly as in *Trachytherus*. *Pseudotypotherium* of the Monte Hermoso[2] differs from *Typotherium* only in having the rostrum less constricted behind the incisors and in the possession of a larger lachrymal foramen. Kraglievich has shown (1930, pp. 146, 147) that both this genus and *Eutypotherium* have two deciduous molars in the lower jaw, thus recording an approach toward the dental formula of *Trachytherus* in the young of these forms.

The upper Miocene typotherids are, as might be expected, much closer to *Typotherium* than to *Trachytherus*. It is, therefore, difficult at this time to follow Lydekker and state definitely that *Trachytherus* is in the direct ancestral line of the Pleistocene genus. It is entirely possible that the Oligocene form may represent a conservative side

[1] Kraglievich (1930, pp. 129–130) has shown that Ameghino (1906, p. 268) and, following him, Rovereto (1914) were incorrect in their belief that the deposits of Laguna Blanca and the Río Fénix were comparable in age to those of the Río Negro.

[2] The genus *Xenotherium* was also described by Ameghino (1904, p. 168) on an isolated I_1 from this horizon.

branch of the family.[1] Knowledge of the lower and middle Miocene typotherids is essential to a decision between these two alternatives. The view that *Trachytherus* represents a stage through which the ancestors of *Typotherium* passed may, however, be safely maintained.

Relationships with the Interatheriidae and the Hegetotheriidae.—*Trachytherus* resembles both the interatherids and hegetotherids in certain characters. Before proceeding to evaluate the resemblances, it will be advantageous to briefly summarize these two groups.

The Interatheriidae are characterized (Sinclair, 1909, p. 2) by rooted median incisors; $I_{\overline{1}}$ not enlarged; epitympanic sinus cancellous; jugal enclosed between zygomatic processes of maxillary and squamosal; carotid foramen close to foramen lacerum posterius; tibia and fibula unfused distally; pes paraxonic; astragalar trochlea bilaterally symmetrical; no naviculo-calcaneal facet. To these may be added the following: upper molars with a united crista and crochet in the median valley; and maxillary with descending process in front of the orbit for the origin of the masseter. The presence of the united crista and crochet is responsible for the bifurcation of the internal fold seen in the molars of *Plagiarthrus* and *Cochilius*. The bifurcation has been lost in *Interatherium* and *Protypotherium*. The cancellous structure of the epitympanic sinus may be regarded as a secondary development since *Cochilius* has the cancellae only slightly developed (Simpson, 1932B, p. 6).

Sinclair (1909, p. 3) distinguished the Hegetotheriidae from the interatherids on the following characters: median incisors rootless; $I_{\overline{1-2}}$ moderately enlarged; epitympanic sinus hollow; jugal orbital; carotid foramen widely separated from foramen lacerum posterius; tibia and fibula fused distally; pes mesaxonic; astragalar trochlea bilaterally asymmetrical; navicular and calcaneum in articulation. The following may be added: jugal and maxillary form a well-developed zygomatic plate extending obliquely upward in front of the orbit for the origin of the masseter. The distal fusion of the tibia and fibula cannot be regarded as a family character, since in *Prosotherium* of the Deseado these bones are separate throughout their length (Loomis, 1914, p. 69). The crown pattern of unworn molars is known only in *Prosotherium*, so far as I am aware. In this genus (Patterson, 1934B, p. 103) the protoloph is joined to the ectoloph by a strong crista, and a second crista connects the

[1] It might be argued that this is probably the case since the contemporary interatherids and hegetotherids were well advanced along the lines of specialization of their respective families. There is no evidence, however, that the rate of evolution of zygomasseteric structure in the Typotheriidae was equally rapid.

ectoloph with a spur extending anteriorly from the internal extremity of the ectoloph. There appears to be no united, prominent crista and crochet such as is noticeable in certain interatherids.

The resemblances of *Trachytherus* to the hegetotherids are as follows: (1) enlarged, rootless, median incisors, (2) incipient zygomatic plate, (3) jugal orbital in position, and (4) bilaterally asymmetrical astragalar trochlea.[1] The genus on the other hand resembles the interatherids in the following characters: (1) presence of a median lobe in the upper molars which is probably composed of an enlarged, united crista and crochet, and (2) small, descending process of the maxillary beneath the orbit.

The points of similarity between *Trachytherus* and the Hegetotheriidae in the skull and dentition, with the exception of the primitive position of the jugal, are such as could have been acquired independently by the two stocks. The Casamayor genera *Isotypotherium* and *Epitypotherium* have nearly symmetrical astragalar trochleae. This would indicate, providing that Ameghino was correct in assigning these genera to the "Eutrachytheridae," that the asymmetrical trochlea of *Trachytherus*, *Typotheriopsis*, etc., was a secondary development.

The points in which *Trachytherus* resembles the interatherids, although few, appear to be more important than those between this genus and the Hegetotheriidae. The three-lobed molar of the later typotherids could have been derived from a molar type similar to that seen in *Plagiarthrus* and *Cochilius* by expansion of the united crista and crochet. *Trachytherus*, in fact, occupies an intermediate position in molar structure between these two types since its molars when newly erupted resemble those of *Typotherium*, while at a certain stage of abrasion they are similar to those of the earlier interatherids. The later typotherids and the interatherids are strikingly different in zygomasseteric structure. Here again, however, *Trachytherus* occupies an intermediate position in that it possesses both a slight descending process of the maxillary and the rudiments of a zygomatic plate. As stated above (p. 125), the genus shows the manner in which the zygomasseteric structure of *Typotherium* probably arose. In addition to this it also offers a clue to the origin of the peculiar modifications of the interatherid arch.

[1] Unfortunately, the astragalus is the only described footbone of *Trachytherus*. In the pes of *Typotherium*, digits II–V are all robust with III the largest and IV only slightly smaller. A calcaneum of *Typotheriopsis* in the Field Museum collections has no facet for the navicular.

The ancestral interatherids probably resembled *Trachytherus* in the possession of a slight descending process of the maxillary beneath the orbit, and a large, stout zygomatic process of this bone which extended posteriorly to articulate with the zygomatic process of the squamosal. In the descendants of these hypothetical forms the origin of the masseter lateralis became concentrated on the descending process, which in some forms, e.g. *Interatherium*,[1] attained considerable size. *Pari passu* with the increase in size of the process the jugal lost its original importance in the zygomasseteric structure and finally became excluded from the facial region and confined to the zygoma.

The fact that the primitive typotherid *Trachytherus* resembles the members of the Interatheriidae in certain important characters, may be regarded as suggestive evidence that these two families are more closely related to each other than either is to the Hegetotheriidae. In the present state of knowledge, however, this view must be regarded only as an interesting possibility that requires testing in the light of future discovery.

MUÑIZIA

Kraglievich (1931, pp. 261–266) described a new genus, *Muñizia*, from the Entrerian with a hegetotherid type of jugal and, according to him, interatherid-like teeth. He referred it to the Interatheriidae as the type of a new subfamily, Muñiziinae. Simpson (1933B, p. 10) considered that derivation of the genus from forms with *Protypotherium*-like jugals would necessitate too great a degree of reversion. He regarded *Muñizia* either as a derivative of the hegetotherids with teeth convergent toward those of the interatherids, or as the representative of a phylum distinct since early Tertiary times.

It is conceivable that the genus is the descendant of early interatherids that possessed a small descending process of the maxillary which was eliminated by their descendants as a result of the later development of a zygomatic plate. It is much more probable, however, that *Muñizia* is a hegetotherid which has retained the tooth pattern of the early members of the family. If the figure of this genus given by Kraglievich be compared with that of the Deseado *Prosotherium* (Patterson, 1934B, fig. 19) the resemblance between the two is at once apparent. In most hegetotherids the

[1] In this genus, probably in correlation with the large size of the process, and consequent increased stress on the anterior teeth, reduction of the dentition has been carried further than in genera with smaller descending processes such as *Protypotherium*.

lingual groove in the upper cheek-teeth was eliminated but the retention of this feature by the ancestors of *Muñizia* would not be at all surprising. Pending further knowledge of the phylogenetic relationships of the early members of the family, the status of Kraglievich's new subfamily must be regarded as doubtful.

SUMMARY

The dentition, skull, and endocranial cast of *Trachytherus spegazzinianus* Ameghino are briefly described. A review of the various opinions that have been offered upon the affinities of the genus is given, and the conclusion reached that *Trachytherus* may be regarded as a primitive typotherid. The known genera of the Typotheriidae are briefly summarized. In view of the hiatus in the history of the family between the middle or upper Oligocene Deseado and the upper Miocene Collon Curá, Río Frías, and Río Mayo, it is impossible to decide at present whether the genus is in the direct ancestral line of *Typotherium* or whether it represents a conservative side branch. A possible mode of origin of the interatherid type of zygomasseteric structure is discussed. Certain characters of *Trachytherus* suggest that the Interatheriidae and Typotheriidae are more closely related to each other than to the Hegetotheriidae.

Muñizia Kraglievich from the Entrerian is regarded as a hegetotherid.

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